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Vascular Plants as Engineers of Oxygen in Aquatic Systems

NINA CARACO, JONATHAN COLE, STUART FINDLAY, AND CATHLEEN WIGAND

The impact of organisms on oxygen is one of the most dramatic examples of ecosystem engineering on Earth. In aquatic systems, which have much lower oxygen concentrations than the atmosphere, vascular aquatic plants can affect oxygen concentrations significantly not only on long time scales but also on time scales of less than a day. Aquatic plants are generally thought of as adding oxygen to aquatic systems through photosynthesis, but the impact of vascular aquatic plants on oxygen varies greatly with plant morphology. Floating-leaved plants that vent oxygen to the atmosphere can strongly deplete oxygen. In some ecosystems where floating-leaved plants have replaced submersed vegetation, oxygen concentrations have been substantially reduced. These oxygen changes can have cascading impacts on nutrient and trace gas chemistry and on the suitability of plant beds as habitat for invertebrates and fishes.

Keywords: ecosystem engineers, vascular aquatic plants, dissolved oxygen

Organisms have dramatically changed the chemistry of Earth (Lovelock 2003). The chemical changes driven by organisms include not only those that have occurred over geologic time scales but also those that occur on short time scales within entire ecosystems or isolated habitats of ecosystems. Regardless of the scale of impact, the chemical changes induced by organisms can alter habitat quality and the availability of resources to other organisms (Baird et al. 2004, Morris et al. 2004, Dybas 2005). These organism-driven chemical modifications, therefore, like the more often considered structural changes driven by organisms, are clear examples of ecosystem engineering (Jones et al. 1997). Of the many chemical changes engineered by organisms, perhaps the most important are the past and present effects of organisms on oxygen levels in the atmosphere, soils, and aquatic ecosystems (Holland 1990).

Since the advent of oxygenic conditions in the atmosphere some 2 billion years ago, oxygen has become essential in the respiratory pathways of eukaryotic organisms, and equally important for many prokaryotes (Fenchel et al. 1998). As a result of this oxygen requirement, many organisms cannot withstand anoxic or even hypoxic (low-oxygen) conditions for extended periods of time (Gray et al. 2002). Moreover, the presence of oxygen allows the juxtaposition of oxic and anoxic environments, and the creation of an interface where chemosynthetic organisms thrive by oxidizing reduced inorganic compounds originating from both biological and geochemical processes (Fenchel et al. 1998). In addition to habitat considerations, the presence of oxygen determines the extent to which some organic compounds are decomposed or preserved, and chemical processes at the oxic–anoxic in-

terface can strongly influence the cycling of limiting nutrients for autotrophic and heterotrophic production, including nitrogen, phosphorus, and iron (Wetzel 2001).

For the past billion years, severe oxygen depletion and anoxia have generally been limited to aquatic systems and water-saturated soils, as oxygen has comparatively low solubility in water. Even when oxygen concentrations are at equilibrium with the overlying atmosphere, there is generally less than 300 micromoles (μmol) oxygen per liter (L) of water, as compared with 8000 μmol oxygen per L of air in the overlying atmosphere (Broecker and Peng 1982). Further, diffusion of gas, including dissolved oxygen, in water is several orders of magnitude slower than in air (Sculthorpe 1967). Because of these two factors, organisms in aquatic systems can influence oxygen conditions strongly not just on long time scales but also over periods of a day or less (Miranda et al. 2000, Caraco and Cole 2002).

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A key determinant of oxygen levels in an ecosystem is the net ecosystem production (NEP) of that system. Net ecosystem production is the difference between gross primary production (GPP) and the respiration of all organisms in an ecosystem (Caffrey 2004). In the absence of significant organic matter loading from outside the system, average NEP is generally positive, and there is a net oxygen release from metabolism (Caraco and Cole 2004). If such a system has substantial burial or export of organic carbon, NEP may be large, and these systems can act as significant carbon dioxide (CO_2) sinks and oxygen sources (Duarte et al. 2004). For systems with external inputs of organic carbon, however, respiration can exceed GPP (Duarte and Agusti 1998, Caraco and Cole 2004), and oxygen concentrations are lowered by this imbalance to levels where external sources of oxygen balance oxygen depletion (Caraco et al. 2000).

Hydrological and physical features strongly influence external inputs of both oxygen and organic carbon. However, organisms can also influence these transfers substantially both by modifying the hydrological and physical features of a system and by directly transferring organic carbon or oxygen, or both, across habitat or even ecosystem boundaries (figure 1). These organism-mediated changes have strong effects

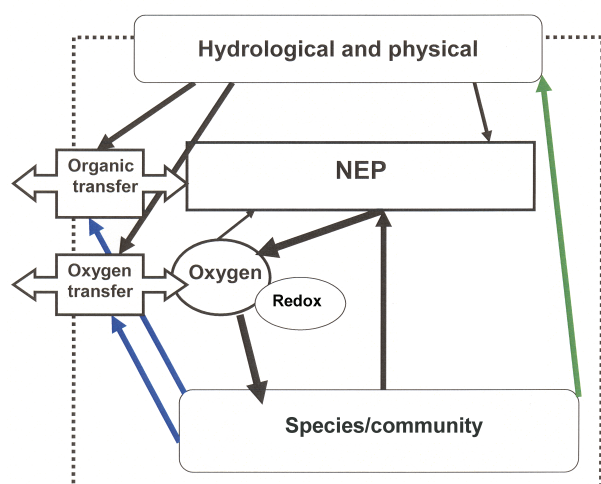


Figure 1. Diagram of species engineering of oxygen levels in ecosystems. The diagram shows the feedbacks of this engineering on habitat and resources through the direct impacts of oxygen levels or through the indirect impacts of oxygen levels on redox chemistry, which can influence nutrient concentrations and ratios. Ecosystem oxygen levels are influenced by the balance of production and respiration within the ecosystem (net ecosystem production, or NEP) and by oxygen transfers across ecosystem boundaries. NEP, in turn, is influenced strongly by transfers of organic matter across the ecosystem boundary. The engineering of oxygen levels by organisms includes not only the direct transfer of oxygen and organic matter (blue arrows) but also the interacting organism-driven alteration of hydrologic and physical characteristics (green arrow) that strongly affect these transfers.

on oxygen levels at scales ranging from major basins of the ocean to millimeter-thick regions in soils and sediments of aquatic systems (Broecker and Peng 1982, Fenchel et al. 1998). A large number of organisms are responsible for altering organic matter and oxygen transfers across ecosystem or habitat boundaries and, thus, engineering the oxygen balance of the system. We focus here on the effect of vascular aquatic plants (VAPs) and in particular on the comparison of completely submersed VAPs with those that have floating-leaved growth forms.

Organic matter and oxygen transport by vascular aquatic plants

Vascular aquatic plants are a diverse group of organisms that dominate the shallows of many lakes, rivers, and estuaries. They act as “hot spots” of metabolism and serve as habitat for animals, algae, and microbes (Kemp et al. 1984, Wetzel 2001, Rascio 2002). The entire group has evolved from terrestrial relatives, contains 33 families (Sculthorpe 1967), and shows large physiological and morphological variation. Two of the key controls on VAPs’ impact on oxygen in aquatic systems are the general growth form (e.g., submersed versus floating) and the extent to which the lacunal system is developed.

The lacunal system in aquatic plants consists of a series of interconnecting gas-filled canals and spaces that are present in most submersed tissue (Sculthorpe 1967). This air-filled system is critical to oxygen storage and transfer between oxygen-producing and oxygen-consuming parts of the plant (Grosse et al. 1996). Aquatic plants vary from those whose growth habitat is completely submersed to those whose photosynthetic tissue is almost all exposed to the overlying atmosphere (Sculthorpe 1967). This distinction is key to the ability of plants to transfer oxygen and organic matter across the ecosystem boundary of the air–water interface (Wilcock et al. 1999, Caraco and Cole 2002).

Regardless of their morphology, all vascular plants transfer organic carbon and some oxygen through various tissues of the plant (Steward 1964, Sorrell 2004). Roots and stems, which often have no photosynthetic capacity, depend on the transfer of organic matter from photosynthetic tissues (Steward 1964). Even tissues with photosynthetic capacity may rely on transfers of organic matter when light is low as a result of high shading and the respiration of plant tissues exceeds GPP. Whether due to shading or to the physiological capacity of the plant tissue, when respiration exceeds GPP, a demand for externally supplied oxygen and organic matter is created. Plants vary greatly, however, in their ability to meet the oxygen demand generated from their own transfer of organic matter (Wigand et al. 1997, Caraco and Cole 2002).

Vascular aquatic plants that are completely submersed can transfer organic material within the confines of the aquatic ecosystem. Thus, for these plants, the presence of a well-developed lacunal system can affect the oxygen and redox status of sediments (Wigand et al. 1997) but not the coupled sediment–water system (figure 2a). Plants with floating or emergent leaves, on the other hand, can transfer

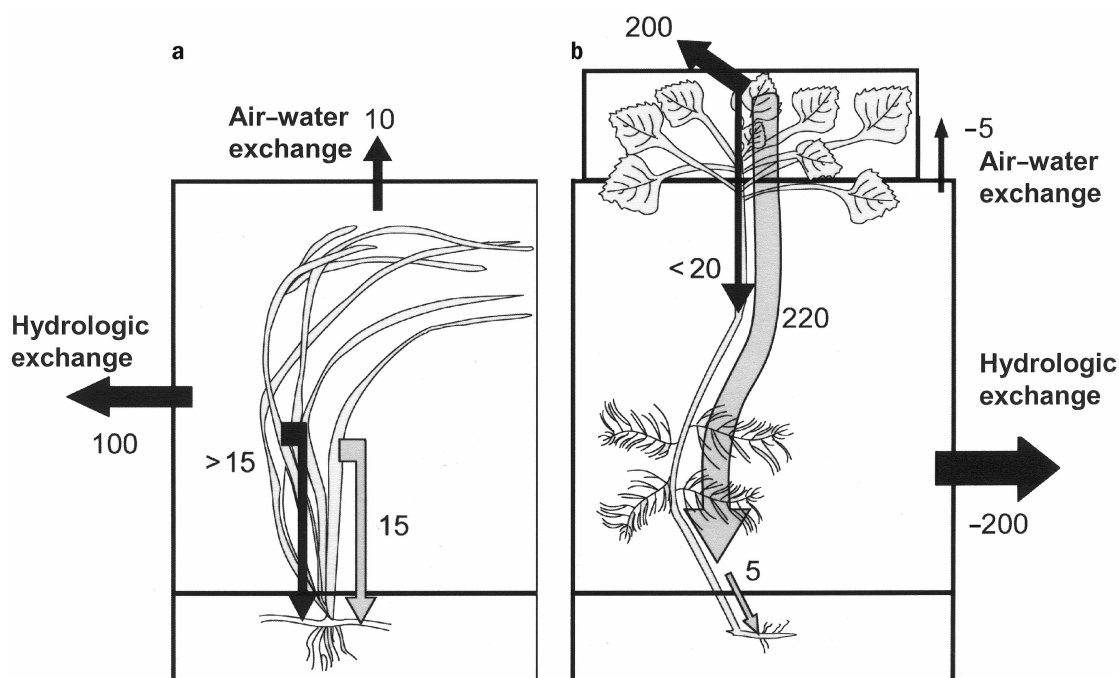


Figure 2. Fluxes of oxygen (black arrows) and organic matter (gray arrows) for (a) a submersed plant (*Vallisneria americana*) and (b) a plant with floating leaves (*Trapa natans*). The transfers of organic matter and oxygen are based on physiological measurements and modeling (Caraco and Cole 2002). All values are in millimoles per square meter per day.

substantial amounts of organic carbon to the aquatic ecosystem from leaves whose photosynthesis occurs in the overlying atmosphere (figure 2b). These floating-leaved VAPs, as a result, have the ability to deplete oxygen not only in sediments but in the aquatic environment as a whole, by importing fixed carbon without the balancing oxygen (Pokorny and Rejmankova 1984, Scheffer et al. 2003). The plants with the highest capacity to consume oxygen are those that form thick mats of floating leaves that inhibit light and GPP within the aquatic system but also have substantial amounts of respiratory tissue submersed below the floating canopy (Caraco and Cole 2002). For these VAPs, the lacunal system can have a large impact not only on sediment oxygen but on the whole ecosystem oxygen balance.

To offset their potentially large oxygen demand, VAPs have the ability to transport large amounts of oxygen through lacunal systems. For example, some floating-leaved VAPs not only have large lacunal spaces but can enhance oxygen transfer through a one-way exchange of gas from young leaves to roots and old leaves (Dacey 1980). This type of enhanced transfer not only greatly increases oxygen transport to the root system but can also enhance reduced gas and volatile metal input to the atmosphere (Grosse et al. 1996, Hamilton et al. 1999). Interestingly, other VAPs with floating leaves have little ability to transfer oxygen to submersed tissues (Pokorny and Rejmankova 1984). Within this category of plants are some important invasive species, including the Eurasian water chestnut (*Trapa natans*), whose introduction into aquatic ecosystems can lead to severe oxygen changes (Caraco and Cole 2002).

Interacting variables and the oxygen balance

The oxygen and organic-matter transfers of VAPs interact with other hydrologic and air–water transfers and with the metabolism of the entire community to determine oxygen levels in the ecosystem (figure 1). These interacting variables may in turn be strongly affected by the physical structure of plants (Jones et al. 1997, Madsen et al. 2001). For some processes, the floating or submersed growth forms are directly linked to interacting effects on oxygen and may predictably affect oxygen surpluses or deficits. In other cases, ecosystem engineering impacts may be determined by structural characteristics of VAPs that are independent of these growth forms.

Hydrologic exchange between vegetated and open waters can greatly modify the chemistry of both vegetated and non-vegetated portions of the ecosystem (Caraco and Cole 2002). In general, open waters have oxygen concentrations that are closer to atmospheric equilibrium than the oxygen concentrations of waters in plant beds; thus, hydrologic exchange tends to moderate oxygen values in beds (figure 3). VAPs tend to reduce this exchange, and plant density and structure influence the extent to which hydrologic exchange is decreased (Thomas et al. 2000, Madsen et al. 2001). It does not appear, however, that the morphological characteristics of plants that determine hydrologic impacts are closely related to the characteristics of plants that determine direct transfers of organic matter and oxygen (i.e., floating versus submersed growth forms and development of a lacunal system).

In addition to bringing in oxygen, hydrologic exchange can carry in dissolved and particulate organic matter. The particulate material, especially, can be trapped within plant beds

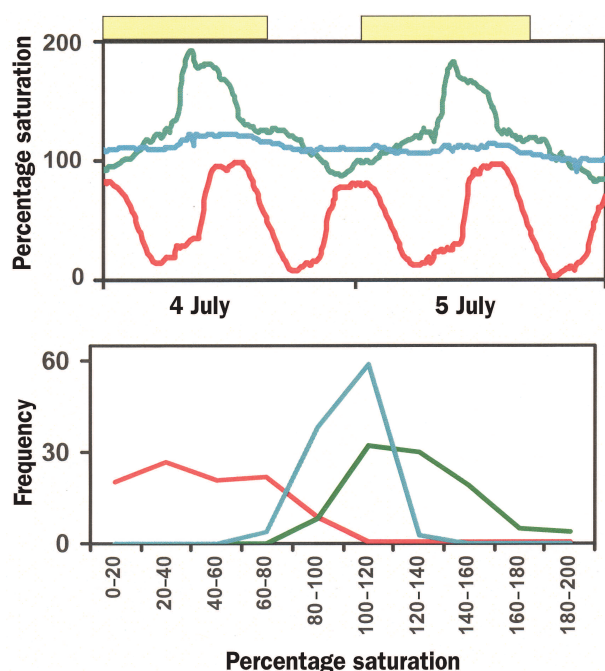


Figure 3. Variation in oxygen between sites in the Hudson River. Sites include an aquatic plant bed dominated by a floating-leaved vascular aquatic plant, or VAP (*Trapa natans*, red); another bed dominated by a submersed VAP (*Vallisneria spiralis*, green); and an open-water site located between the two beds (blue). Upper panel: Variation in oxygen for two days in summer 2003, with days starting at sunrise and periods of sunlight designated by yellow bars. Oxygen is shown in saturation with respect to atmospheric equilibrium (about 320 micromoles for temperatures on these days). Lower panel: Frequency of oxygen values observed in the three beds during a month of summertime monitoring (20 June–20 July 2003).

as a result of reduced water currents. Thus, the same characteristics of plant beds that determine the delivery of oxygen from surrounding waters can strongly influence particle trapping (Madsen et al. 2001). The filter-feeding biota inhabiting aquatic plant beds can have an important influence on particle trapping as well (Agawin and Duarte 2002). In either case, the trapped material can increase sedimentation, serve as an important food source for animals and protozoans residing in plant beds, and affect the oxygen within aquatic plant beds. That is, upon respiration, trapped material can consume considerable amounts of oxygen and, in extreme cases, could alter the balance of an aquatic plant community from one that produces oxygen to one where there is a net consumption of oxygen.

Exchange with the atmosphere, like water exchange, can act as an important source or sink of oxygen to plant beds and can moderate the effects of positive or negative NEP. In aquatic systems, oxygen exchange is determined by the deviation of the aquatic system from atmospheric equilibrium val-

ues and by physical exchange velocities that vary with turbulence at the air–water interface (Turney et al. 2005). This turbulence, in turn, is influenced by both wind and current, but can also be influenced by aquatic plant growth form and density. In particular, dense growth of plants with floating vegetation not only reduces the water surface area available to exchange but also lowers turbulence in water not covered by vegetation (Scheffer et al. 2003). Thus, a potentially negative oxygen balance generated by high organic matter transfer in floating-leaved plants may be exacerbated by low atmospheric exchange (Caraco and Cole 2002).

The community of organisms associated with VAPs is diverse and includes both autotrophic and heterotrophic members (Wetzel 2001). Periphyton (algae residing on the stems and leaves of aquatic plants) are an important autotrophic component of VAP beds. Periphyton are an important food source for many consumers in the macrophyte beds (Cattaneo et al. 1998), and their GPP adds oxygen to the water, which may alter the oxygen balance of systems. However, this GPP, like that of the aquatic plants themselves, relies on light, and in dense beds of floating-leaved macrophytes, periphyton may have only very low biomass and production (Cattaneo et al. 1998). On the other side of the oxygen balance are heterotrophic microbes and animal consumers, which can add a significant respiratory demand to aquatic ecosystems (Caraco et al. 2000). Although extended hypoxia in some large plant beds with floating leaves could reduce the abundance of some sensitive organisms (Dybas 2005), many microbes, protozoans, and invertebrates can withstand hypoxia or even anoxia for extended periods of time, and it is not clear that plant beds with floating growth forms generally have fewer heterotrophic animals or less respiration associated with heterotrophic community (Strayer et al. 2003).

Animals can not only trap organic matter within aquatic plant beds but also play a role in the transfer of organic matter and oxygen within the system. Some sediment-dwelling organisms, through burrow formation and active pumping of water, can play a role in oxygenating sediments and creating microzones of high biogeochemical activity (Riisgard and Larsen 2005, Gutiérrez and Jones 2006). Other organisms aid in the deposition of organic matter (Strayer et al. 1999) without increasing oxygen delivery to sediments, and thereby lead to more reducing conditions in sediments.

Aquatic plant beds as biogeochemical hot spots

In many ecosystems, biogeochemical reactions, rather than occurring uniformly, are concentrated in “hot spots” in the landscape (McClain et al. 2002). Biogeochemical hot spots vary in size from microzones surrounding animal burrows to the large, low-oxygen midwaters of the oceans. Across a range of scales, many hot spots are characterized by strong oxygen gradients. Aquatic plants, through their production, consumption, and transport of oxygen, can generate strong oxygen gradients in space and time and be engineers of redox-related biogeochemical hot spots.

Both submersed aquatic plants and floating-leaved plants with substantial oxygen transport can generate oxidized zones in otherwise reduced sediments (Dacey 1980, Wigand et al. 1997). These oxidized microzones are often only a few millimeters thick, and diffusion across these zones readily mixes reduced inorganic compounds with more oxidized compounds, including oxygen. Oxidized microzones are critical in regulating redox processes, including coupled nitrification–denitrification, which reduces the nitrogen content of ecosystems and generates important greenhouse gases (Fenchel et al. 1998, Cole and Caraco 2001). In addition, oxidized microzones can concentrate metal oxides such as iron to the extent that visible plaques can form around the roots of VAPs (Christensen and Wigand 1998). These plaques, in turn, can play critical roles in concentrating not only other metals but also phosphorus, an often limiting nutrient for plant growth. Some plants use this trapped phosphorus, often with the aid of mycorrhizae (Wigand and Stevenson 1997).

In addition to the sedimentary hot spots, the water column can have redox-related hot spots associated with alternation between oxic and anoxic conditions. These alternating conditions can be due to variations in the metabolic balance of the system at seasonal or even diel time steps (Miranda et al. 2000), or with regular (e.g., tidal) or irregular mixing (e.g., floods) of oxic and anoxic waters (Caraco and Cole 2002). Mixing of water between aquatic plant beds and open waters creates biogeochemical hot spots and serves as a mechanism to export the ecosystem engineering impacts of plants to the open waters of aquatic systems (Caffrey 2004). These changes can include the oxygen balance of the open-water environment as well as nutrient concentrations and ratios and greenhouse gas concentrations (Caraco et al. 2000, Cole and Caraco 2001). A dramatic example of this systemwide impact has been documented in the Paraguay River, which has adjoining wetlands inhabited by a thick growth of emergent and floating-leaved aquatic plants (Hamilton et al. 1997). For this system, oxygen in the entire large river system was reduced to near zero, while CH₄ (methane) and CO₂ increased dramatically, coincident with the seasonal flooding of the adjoining Pantanal wetlands (Hamilton et al. 1997).

Habitat impacts

The impact of low oxygen on aquatic organisms is well studied, as low oxygen conditions have been demonstrated to be a serious and growing problem in lakes and estuaries, associated with eutrophication by organic matter or inorganic nutrients (Dybas 2005). Low oxygen is generally not thought to be a result of ecosystem engineering by aquatic plants, because these plants are usually thought of as providing oxygen to aquatic environments. Aquatic plants can, however, engineer not only high oxygen values but extremely low values as well. These low-oxygen events can occur daily in some very dense macrophyte beds or in association with macrophyte decay at the end of growing season, but can also be a direct result of organic matter redistribution during the growing

season. This same season is often critical for fish and invertebrates relying on macrophyte beds for habitat. When low oxygen values occur in plant beds, many organisms may be eliminated from habitats altogether (Dybas 2005). Others employ behavioral or physiological adaptations in response to low-oxygen events (Gray et al. 2002, Strayer et al. 2003). For systems that alternate between oxic and anoxic events, highly mobile organisms, such as fish, may respond by moving between plant beds and open waters with higher oxygen or by finding microrefuges of higher oxygen within the plant bed (Miranda et al. 2000).

In addition to direct impacts of low oxygen, many of the chemical changes related to or brought about by low oxygen can also influence organisms. High CO₂ levels associated with negative NEP can have serious negative impacts on fish (Caraco et al. 2000). These same high CO₂ levels, when exported to neighboring open waters where phytoplankton production dominates or to adjoining beds of submersed aquatic plants, can potentially alter the GPP and stoichiometry of producers in surrounding waters (Urabe et al. 2003, Schippers et al. 2004). The changes in metals and nutrients that occur in low-oxygen conditions or at oxic–anoxic boundaries can also influence primary producers in surrounding waters. For example, the low ratios of nitrogen to phosphorus that may occur under these conditions can select for nitrogen-fixing cyanobacteria, which may be favored by low nitrogen availability (Smith 1983). As these cyanobacteria can be toxic or have low palatability compared with other phytoplankton, this change can cascade through the planktonic food web and may even influence human use of the system (Paerl 1988).

Human impacts on system engineering: The case of the Hudson River

Through introductions or changes in habitat availability caused by hydrologic changes, dredging, or nutrient pollution, humans have altered not only the abundance of aquatic plants but also the species of plants present (Scheffer et al. 2003, Hummel and Kiviat 2004). Because different aquatic plants can engineer oxygen in different ways, these human-induced changes can also influence the chemistry and habitat quality both of the specific plant beds and of the entire river system. The tidal Hudson River represents a case where the dominant introduced and native species of aquatic plants engineer oxygen in the plant beds in completely different ways. Moreover, because of the tidally driven exchange of water between plant beds and open waters, the effects of different plants extend beyond the realm of the plant beds to the aquatic ecosystem as a whole (Caraco et al. 2000).

The shallows of the tidal Hudson River are dominated by two aquatic plants that occur in distinct, nearly monospecific beds (Nieder et al. 2004). *Vallisneria americana* is a native submersed VAP. *Trapa natans* is an introduced Eurasian floating-leaved VAP. For these two plants, the balance of carbon and oxygen transfers is very different (figure 2). Largely as a result of these different transfers, diel oxygen dynamics in plant

beds dominated by *T. natans* and *V. americana* are dramatically different during the summer growing season (figure 3).

Oxygen levels in large *T. natans* beds alternate between oxic and hypoxic levels (below 60 μmol) that are harmful to both sensitive fishes and invertebrates (Gray et al. 2002). Simultaneous with the oxygen decline in these beds are other chemical changes with habitat and ecosystem consequences (figure 4). For example, CO_2 concentrations increase by more than 10-fold, to nearly 400 μmol (more than 20-fold atmospheric equilibrium values), and ratios of dissolved nitrogen to phosphorus decline from 200% to 20% of the 16:1 ratio required by many phytoplankton and aquatic plants (Broecker and Peng 1982). The chemical changes in *V. americana*, where hypoxia does not occur, were very different in both magnitude and direction (figures 3, 4). Most of the chemical differences between beds are brought about by the cascading impacts of hypoxic conditions or alternating oxygen conditions in *T. natans* beds.

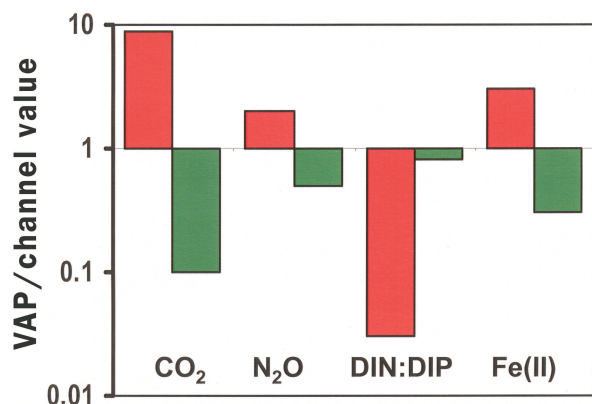


Figure 4. Contrasting chemical impacts of floating-leaved (red) and submersed (green) vegetation in the Hudson River. Values are expressed as the ratio between concentrations in the bed at low tide and adjacent channel values. Values less than 1 represent depletions in the bed, while values greater than 1 are enrichments. Note the log scale. Abbreviations: CO_2 , carbon dioxide; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Fe, iron; N_2O , nitrous oxide; VAP, vascular aquatic plant.

Species introductions in the Hudson are widespread, as in many other aquatic systems, and several of these introductions have had substantial ecosystem impacts that have been well studied (Strayer et al. 1999). The context for understanding species invasions, for both ecologists and managers, has primarily been through food web interactions. It is becoming clear in the Hudson, and in many other systems, that important ecosystem impacts of invasive species can occur through ecosystem engineering (Wright and Jones 2006). This engineering includes strong changes in the chemistry of the environment (Vitousek et al. 1997, Vanni 2003). To date, generalizations about the chemical impacts of invasive species lag behind predictions of their impacts on food webs

(Carpenter et al. 1992, Vander Zanden et al. 1999). It is likely that many of the chemical changes engineered by invasive organisms will not be predicted well by broad taxonomic features or even by trophic position. Better predictors may be features such as the balance of organic matter and oxygen transference to a system.

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